

PARASITISM OF ORDOVICIAN BRYOZOANS AND THE ORIGIN OF PSEUDOBORINGS

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ABSTRACT. Upper Ordovician trepostome bryozoans from the vicinity of Cincinnati, Ohio, USA, contain trace fossils that resulted from the overgrowth by the bryozoan of soft-bodied parasites that settled on the living colony. The resulting structures (pseudoborings) superficially resemble borings, and the term 'bioclaustration' is introduced to describe the process. The pseudoboring consists of groups or rows of sub-circular pits, connected by tunnels that were formed by the roofing-over of adventitious stolons by localized bryozoan growth. The structure reflects the external morphology of the parasite, and is named *Catellocaula vallata* ichnogen. and ichnosp. nov. A hydroid or colonial ascidiacian tunicate is suggested as the perpetrator.

THE study of trace fossils in the Upper Ordovician rocks in the vicinity of Cincinnati, Ohio, where minimal diagenetic overprinting and exquisite preservation rival anything that can be found in the European Mesozoic, has largely concentrated on burrows and trails (Osgood 1970). Although the hard substrate trace fossils have received passing mention from a number of workers (Palmer 1982; Wilson 1985), there have been no detailed studies of the borings that are found abundantly in organic and inorganic hard substrates.

By far the most common of these borings is *Typanites*, which is found in the massive skeletons of bryozoans, corals, and stromatoporoids; in the thin shells of molluscs and brachiopods; and in cobbles and hardgrounds. *Trypanites*, which undoubtedly represents the dwelling tubes of a variety of filter-feeding worms, is extensively known from other Ordovician rocks throughout North America and Europe (Kobluk *et al.* 1978). Of far more limited geographic extent, apparently limited to the Lower Cincinnati of the type area, is the groove-shaped boring first described by Pojeta and Palmer (1976) and ascribed to the rasping activity of the modiomorphid bivalve *Corallidomus scobina*. These borings, named *Petroxestes pera* by Wilson and Palmer (1988), occur solitarily or as aggregated clusters in cobbles, hardgrounds, and massive skeletons.

But if borings have received short shrift relative to soft-sediment trace fossils in the Upper Ordovician, how much more so has the second class of hard-substrate trace fossil, formed by biological infestation of a living host that subsequently adapted its growth to enclose and isolate the infester. Such embedment structures are generally acknowledged to be a class of trace fossil (Müller 1962; Bromley 1970; Conway Morris 1980; Ekdale *et al.* 1984), but are easily mistaken for borings because they end up as holes in the skeleton of the host. The walls and rims of such holes must be closely examined for signs that the skeletal elements and growth lamellae of the host are distorted around the hole, rather than cut by it. Only thus can such pseudoborings be distinguished from true borings. Bromley (1970) discussed several examples of such embedment structures, and pointed out that in some cases, elements of both embedment and boring can be seen in the same structure. Borers, for example, may break through the inner surface of the shell of a living bivalve, and cause it to cover the intrusion with a blister of carbonate, secreted by the outside face of the mantle. Similarly, embedded parasites may enlarge their holes by boring, in order to accommodate growth or erosion.

The process of embedment of a soft-bodied infesting organism by skeletal growth of its host is called by us 'bioclaustration' (biologically claustrated, or enclosed behind a wall, cloister, or rampart). The unequivocal example of this process that forms the subject of this paper is the earliest yet described in detail, and the only example so far elucidated that involves fossil bryozoans.

Recognition of bioclaustration in the fossil record requires the host organism to be skeletonized. The infester, probably parasitic but conceivably mutualistic (see discussion below) is, by definition, soft-bodied. Comparable growth interactions may take place between two skeletonized taxa, to produce skeletal intergrowths (e.g. between Palaeozoic stromatoporoids and corals—see Kershaw 1987; Mistiaen 1984) but we do not regard such interactions as examples of bioclaustration, even if the infester is much smaller than the host and locally embedded in it, rather than inextricably intergrown. An example of this situation is provided by tube-secreting worms that embed within living coral and lengthen to keep pace with its growing surface, or by cornulitids that settled on Silurian crinoid stems and became embedded by excessive calcite secretion (Franzén 1984). Bioclaustration structures, in contrast, are trace fossils and are recognized only by the disturbance caused to the growth of the host.

Bioclaustration is not to be confused with bioimmuration. The latter involves two sessile organisms, one soft-bodied and one calcified, growing alongside one another. Crowding may result in the skeletonized neighbour overgrowing the other, and moulding its attachment surface over the soft-bodied competitor. Bioimmuration thus demonstrates chance competition for space, not a response to an interaction that is of one of the partner's seeking.

EXAMPLES OF BIOCLAUSTRATION

Reports of bioclaustration in the fossil record are few and far between, but span the Phanerozoic. Scrutton (1975) reported Jurassic, Cretaceous, and Tertiary serpulid worm tubes that claustrate the stoloniferous hydroid *Protulophila gestroi* Rovereto. Scrutton speculated that the relationship could have been of mutual advantage, the worm conferring both substrate and an increased supply of suspended food particles, and the hydroid offering the protection of its nematocysts.

There is a more extensive literature on the formation of gall-like structures in echinoderms, caused by an irritating infester leading to secretion of adventitious stereom in an attempt to isolate the irritant. Franzén (1974) and Brett (1978) have reviewed such examples and added further data on Silurian and Devonian crinoid infestation. Some examples demonstrate a response to encrustation by shelly fossils (cornulitids, crinoids, bryozoans, forams) but others show only pits or cavities within the swellings and appear to represent bioclaustration.

Bromley (1970, p. 50) has reviewed examples of embedment in the fossil record, and has noted that some holes traditionally ascribed to borings show distributions and morphologies more in keeping with bioclaustration structures. Chatterton (1975) has described bioclaustration by Devonian spiriferids of a soft-bodied filter-feeder that settled on the growing valve margin and extended its feeding crown into the inhalant feeding currents within the mantle cavity of the host. The brachiopod responded by secreting a cylinder of shell material around it, now preserved as a small, calcite, inwardly projecting chimney. This relationship did not involve penetration through the shell by a borer that encountered protective secretion only when it broke through to the inside of the shell and irritated the living mantle surface. There is an extensive literature on this latter phenomenon, with many recent examples that have commercial implications in shell-fishery (see references quoted in Boucot 1981). We regard such cases as modified borings, not examples of bioclaustration, and the resultant traces can usually be ascribed to the same ichnotaxa as examples of the same borings that do not break through the shell and irritate the host (Bromley 1970). The results of bioclaustration, in contrast, constitute their own category of trace fossil and require their own ichnotaxonomy. Incidentally, of course, the holes resulting from this type of embedment accurately reflect the external shape of the infesting organism and may point to its zoological affinities.

INTRASPECIFIC RELATIONSHIPS

The recognition of the precise nature of an interaction between species in the fossil record is difficult. In living organisms, recognition of parasitic, as opposed to proto-co-operative or

mutualistic interactions, can be made by assessment of growth rates and population dynamics in associated versus independent species (e.g. Osman and Haugsness 1981). Such options are not open to palaeontologists, whose assessment of the cost-benefit analysis must be based on limited observation tempered with common-sense. Subtle details of an interaction cannot be observed, and should not be surmised if parsimony is to be maintained. However, some general principles apply.

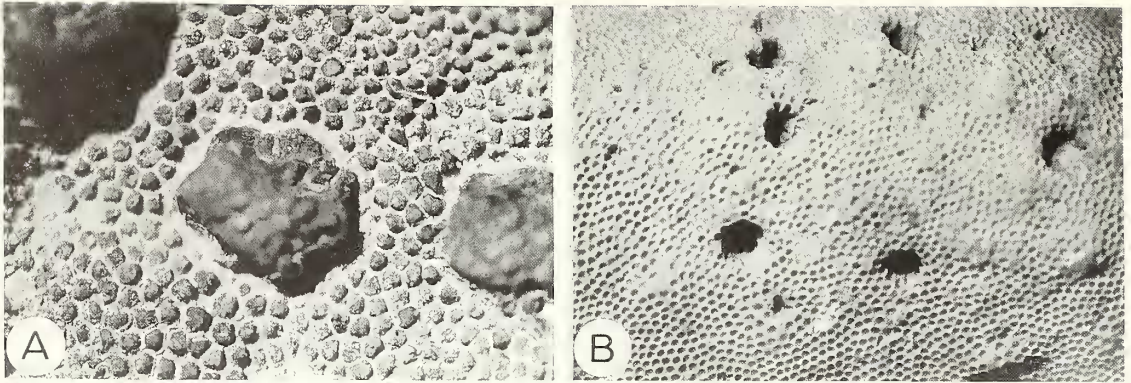
Any interaction that promotes a growth response in one of the parties is energetically costly. An infestation that eliminates some of the members in a colonial organism further reduces food intake and limits fecundity. In such cases, the infester is presumably advantaged because it is the infester that initiates the contact. Such relationships should be regarded as being of a $+/-$ nature, and hence parasitic, unless the advantages conferred upon the host outweigh these disadvantages. We might reasonably expect that examples of a particular pairwise interaction would be more common if of mutual benefit, than if only to the advantage of one of the parties involved. This is because selection may be expected to favour the attraction and conjoining of the two species involved. The end evolutionary result of such cases is mutualism, in which the interaction is obligatory for both parties. This is not to say that heavy infestation of a host by a parasite may not occur in some host populations, but it is not unreasonable to infer that low levels of infestations, in which there is clear evidence of morphologic damage to the host, are more likely to represent examples of parasitism than a $+/+$ interaction. The association that forms the subject of this paper is only seen in a few percent of the individuals of the species of bryozoan involved. The advantages that accrued to those few individuals may have outweighed the disadvantages, but we think it is much more likely that this was not so, and that we are dealing with a case of ectoparasitism. Our vocabulary in the following section will reflect this belief.

INFESTATION OF CINCINNATIAN BRYOZOA

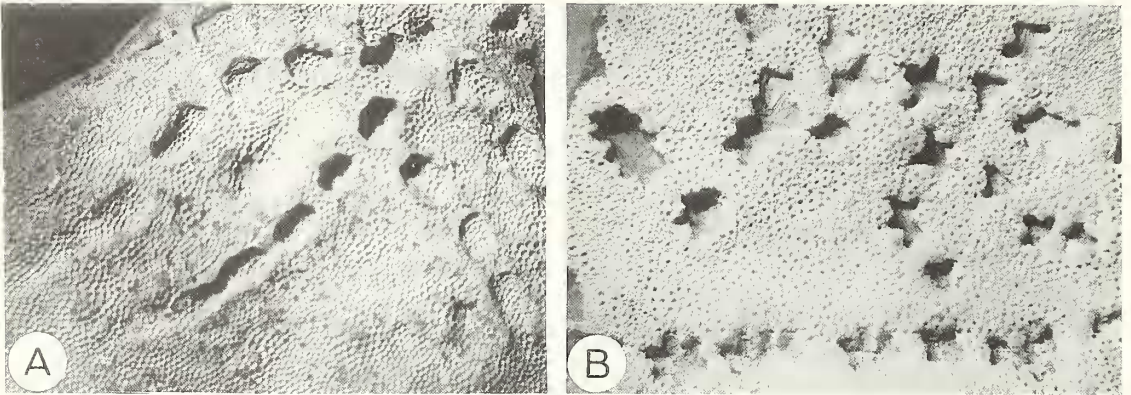
Borings and pseudoborings

The Upper Ordovician rocks that occur around Cincinnati in south-west Ohio, USA, and in the adjacent parts of the neighbouring states of Indiana and Kentucky, consist of interbedded soft silty and bioclastic limestones. Aragonitic taxa have been dissolved out in both lithologies, but skeletons of original calcite are virtually unaltered. Amongst the calcitic groups, bryozoans weather out of the sections in great profusion, and can be collected in large numbers. Many zoaria show signs of boring by the worms that produced *Trypanites*, usually as post-mortem colonization. A few specimens indicate infestation of the living bryozoan (as evidenced by a growth response of the adjacent zooecia). *Trypanites* occurs as circular holes, up to 2 mm across, penetrating the bryozoan skeleton. Many such holes may occur on a single fragment.

In the Kope Formation at the base of the Upper Ordovician sequence, bryozoans of the genera *Amplexopora* and *Peronopora* contain a different structure that looks to the unwary eye like an array of equispaced *Trypanites* that differ from the norm by the fact that their inner margins are slightly crenulate to stellate. However, when a recently collected specimen of *A. persimilis* Nickles, 1905 (from Mr B. Bodenbender) was examined closely, the pits were seen to be part of a single structure. This was suggested by their regular spacing (2–3 mm apart), and the fact that in the outer parts of the array the pits define straight or gently curving lines, four or five pits long, terminating in an elongate shallow groove. The integral nature of the pit array was confirmed by sectioning, which revealed buried tunnels that join the bases of the adjacent pits in each line. The crenulate margins of the pits are formed by the walls of the zooecia that surround them (Pl. 87, fig. 1). They may be somewhat thickened and, in well-preserved specimens, they are raised slightly above the surface of the surrounding zoarium (text-fig. 1A). This feature suggests that the holes are, at least in part, pseudoborings that represent reaction by the bryozoan. In contrast, *Trypanites* that are inferred to have been excavated post mortem exhibit sharp truncation of the zooecia and do not show raised rims (text-fig. 1B).



TEXT-FIG. 1. Difference between bioclaustration structures and borings in Ordovician trepostomes from the Upper Ordovician, Kope Formation, near Cincinnati, Ohio, USA. A, pits of *Catellocaula vallata* ichnogen. and ichnosp. nov., formed by bioclaustrating growth of host bryozoan, showing pit margin and slightly thickened raised reaction rim; note that the zooecia adjacent to the pit are not truncated. USNM 419444, $\times 13$. B, borings (*Trypanites*), showing truncation of zooecia. USNM 419476, $\times 6$.

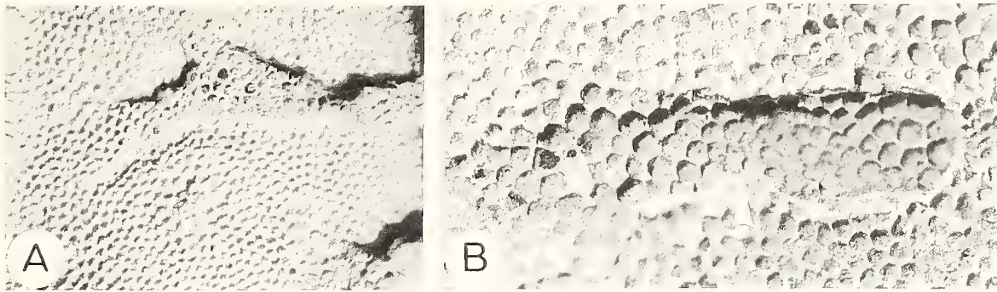


TEXT-FIG. 2. *Catellocaula vallata* ichnogen. and ichnosp. nov. in Ordovician trepostomes from the Upper Ordovician, Kope Formation, near Cincinnati, Ohio, USA. A, part of USNM 419444, in *Amplexopora persimilis*, showing three lines of pits each terminating distally in a groove, $\times 2.9$. B, part of USNM 419462, in *Peronopora* sp., showing pits with crenulate margins, $\times 4.4$.

Formation of the pseudoborings by bioclaustration

The pseudoborings consist of four interconnected elements: pits, grooves, galleries, and tunnels. Pits and grooves are visible as holes or indentations in the exterior surface of the bryozoan (text-fig. 2). Galleries and tunnels respectively represent pits and grooves that have been roofed over by bryozoan growth, and are only seen in cut sections. The soft tissue of the parasite was originally continuous throughout the four structures, each of which represents a unique combination of interaction between bryozoan growth pattern and different parts of the parasite's body.

The floors of all four of the structures that constitute the pseudoboring are located at the same level within the bryozoan zoarium, and invariably mark a growth interruption. These interruptions are usually interpreted as having been caused by local damage to the surface and cessation of growth of the bryozoan, with rupture of exterior membranous colony walls (Boardman 1983, p. 129). They are easily recognized by the thickened zooecial walls immediately below the interrup-



TEXT-FIG. 3. *Catellocaula vallata* ichnogen. and ichnosp. nov., showing grooves which terminate lines of pits. A, USNM 419449. Bifurcating groove, $\times 4.6$. B, USNM 419444, showing constriction (arrowed) where groove walls roof over to isolate new pit proximally, $\times 11.5$.

tion, upon which the pseudoboring sits. In adjacent regions, renewed growth of the zooecia above the interruption shows up as a zone marked by thin zooecial walls that sit upon, and contrast markedly with, the thick walls below (Pl. 87, fig. 2). Whether the damage that initiates these intra-colony overgrowth surfaces is external and merely exploited by the parasite, or whether the parasite causes the damage in the first place, is discussed below.

Pits. Pits are *c.* 2 mm in diameter and *c.* 1–2 mm deep. Their floors are formed by the zoarial surface below the intra-colony overgrowth surface, and their walls by the walls of the zooecia that grew up around them and which become more thickened upwards. These walls are vertical, or slightly divergent upwards as adjacent zooecia lean away from the pit centre (Pl. 87, fig. 3). Examples in *Amplexopora* show that the walls are slightly fluted vertically and, when well preserved, rise just above the surface of the surrounding zoarium to form a reaction rim (text-fig. 1A). The fluting on the walls gives this rim a crenulated rather than a perfectly circular outline. Examples in *Peronopora* show much better development of the crenulations, so that the pits become stellate (text-fig. 2B).

In the older (more central) parts of mature colonies, the pits are more or less equispaced, their centres 2–3 mm apart. Towards the periphery they line up in straight or gently curving rows, two to five pits long (text-fig. 2). The rows usually terminate in grooves. The older pits in the central parts tend to be deeper than those towards the edges as a result of upward growth of the surrounding zooecia.

Grooves. Grooves have the same width as pits, but are up to *c.* 10 mm long (text-figs. 2A and 3). They are straight to gently curving and may bifurcate. They are deepest at their proximal ends (*c.* 1 mm) and shallow distally, becoming flush with the exterior surface of the zoarium. Where deepest, their walls are thickened to produce a reaction rim. Grooves develop into lines of pits by localized ingrowth of bryozoan zooecia on either side. These ingrowths roof over the top of the groove, meeting one another and thereby isolating the proximal end of the groove as a new pit. Some grooves show the start of this process as a constriction *c.* 2 mm from the proximal end (text-fig. 3B).

Tunnels. Tunnels join adjacent pits along a single line, and their floors lie at the same level along an intra-colony overgrowth surface as the pit floors. They developed by local encroachment of the bryozoan across grooves, thus pinching off new pits that retained a soft-tissue connection with the truncated groove (and with each other) via the tunnels (Pl. 87, fig. 4). Some pits have such connections with two distal neighbours and represent overgrowth of a bifurcating groove. This method of tunnel formation is clearly critical to the recognition that these are bioclaustration structures rather than borings. Sections through tunnels show that the roofs are formed by oblique lateral walls of adjacent zooecia which spread out by lateral budding from those adjacent to the

groove margin. They are not truncated (Pl. 87, fig. 5). Although such ingrowth seems to take place from both sides of the groove simultaneously, no obvious suture is formed where the two sides meet.

Tunnels are often filled with mud matrix, as are pits and some of the zooecial living chambers immediately below the intra-colony overgrowth surfaces within the bryozoan. However, a few tunnels seem to have become occluded by a meshwork of curved diaphragms which together form a plug (Pl. 87, fig. 6). The plugs kept out mud, and the spaces between the diaphragms are now filled with large equant crystals of calcite spar. We discuss the origin of these tunnel diaphragms below.

Galleries. A few specimens show pits that have been roofed over by an encroachment process similar to that which gives rise to the tunnels. Such galleries are encountered in sections, or rarely indentified on the surface where their roofs of delicate, oblique zooecia have been crushed and impressed into the underlying space.

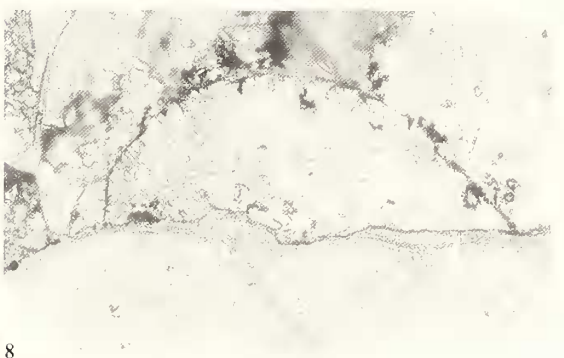
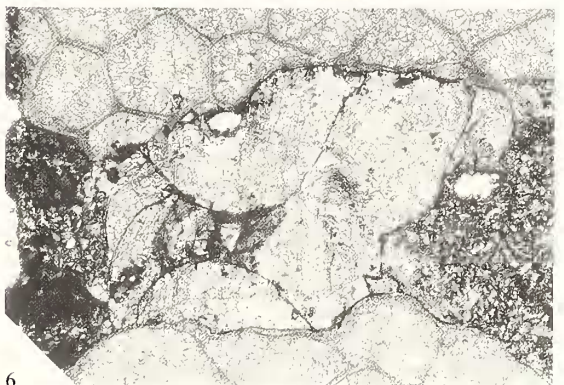
Host-parasite interactions

Pseudoboring lining and tunnel diaphragms. The lining of the pseudoboring is marked by a thin membrane that is continuous over the inner surface of the tunnels and pits in well-preserved specimens (Pl. 87, fig. 7). We conclude that it was originally present in grooves and galleries as well, but we have not seen enough sections through unabraded examples of these structures to be sure. The membrane marks the original outer surface of the parasite. It is thin (considerably thinner than zooecial walls and diaphragms) and, in acetate peels, shows minute irregular brown blobs along its length that are probably remnant organic material or oxidized pyrite. It drapes over the upstanding walls of the zooecia beneath (Pl. 87, figs. 7 and 8). Where stretched across the apertures of these zooecia, it appears to have prevented access of sediment into their lumina. Sediment-filled zooecia have lost this coating membrane. On tunnel roofs the membrane lies against the outside of the oblique walls of the overlying zooecia.

Within tunnels the curving diaphragms of the tunnel plugs insert on to the surface of the membrane (Pl. 87, fig. 8) and appear to be made of the same material. The diagenetic calcite that fills the spaces within the plug consist of one or a few large crystals, rather than drusy calcite which typically fills the spaces within the bryozoan zoarium. Drusy texture is controlled by the presence of seed crystals in the walls, upon which the precipitating cement can initiate. Absence of this texture within the plugs suggests that the diaphragms, unlike the bryozoan skeletal tissue, are not of an original calcite composition.

EXPLANATION OF PLATE 87

Figs. 1-8. *Catellocaula vallata* ichnogen. and ichnosp. nov. USNM 419461. Acetate peels of cut and polished surfaces through *Amplexopora persimilis* to show relationships between the bryozoan skeleton and the parasite, Newport Shopping Center, Ky., USA, Kope Formation, Edenian. 1, tangential section through pit, showing that pit wall is formed by zooecial walls (arrowed), $\times 48$. 2, longitudinal vertical section through tunnel, showing that tunnel floor is not bioerosive, but sits upon thickened zooecial walls along an intra-colony overgrowth surface, $\times 108$. 3, transverse vertical section through zoarium between two pits (upper right and left) showing deflection of growth of adjacent zooecia away from pits, $\times 48$. 4, longitudinal vertical section through tunnel between adjacent pits along a line; right-hand pit is filled with dark sediment, $\times 46$. 5, close-up of fig. 4 showing that roof of tunnel is formed by walls of oblique zooecia (arrowed) that overgrow from the sides, $\times 112$. 6, longitudinal tangential section through tunnel showing curved diaphragms of the tunnel plug, $\times 48$. 7, oblique vertical section through tunnel showing dark bounding membrane (arrowed) draping over upstanding zooecial walls on tunnel floor, and overgrown by oblique zooecia of tunnel roof, $\times 105$. 8, close-up of fig. 6 showing thin dark tissue of tunnel diaphragm (upper arrow) joining bounding membrane that lines tunnel wall (lower arrow), $\times 134$.



There are two possible origins for this organic membrane. It may represent remnants of the cuticle of the bryozoan. Trepostome cuticular appearance is poorly documented, but similar structures have been described and illustrated by Boardman (1973). If it is of bryozoan origin, then it might also be expected to be visible over the external surface of the zoarium, or covering zoecia that have mounded up around the mouths of *Trypanites* borings that were excavated while the colony was still alive. Our research for the membrane in these circumstances, though not exhaustive, has been unsuccessful. The alternative is that the membrane was laid down as an outer integument by the outer surface of the parasite. The use of a meshwork of membrane material to form the tunnel plugs seems to us somewhat more in keeping with this second explanation. The tunnels originally contained stolon tissue that was important in vegetative growth and reproduction of the parasite (see below), but not necessary for everyday function. Once their purpose had been achieved, they could be infilled.

Settlement and growth of the parasite. Initial infestation of the bryozoan surface occurred at a single point. Some examples show that the bryozoan could respond rapidly, resulting in a single pit. There is some indication that these single pits coincide with the position of maculae on the bryozoan surface, but we have not seen enough unequivocal examples to be sure. These cases showing an immediate response of the bryozoan, claustrating the newly settled parasite before it had time to grow, suggest that the adjacent zoecia were alive and able to respond rapidly. This supports a contention that the parasite settled on a live area of the zoecium, and gained access to the host by its own activities. If it had settled on a larger expanse of dead zoarium, claustration could not have commenced until living bryozoan tissue had invaded from the edges of the dead area, and the distal parts of the infester are likely to have had time to grow and to have been claustrated before the central part.

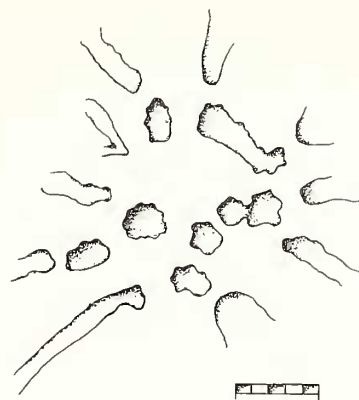
Having become established, the parasite sent out ribbon-like stolons of adventitious tissue radially in several (usually three or four) directions. As these grew distally, away from the ancestral pit, they came to lie in grooves as bryozoan zoecia grew up to flank them. Proximal ends of grooves are deeper than distal ends because the parasite tissue within them was older, and more zoecial growth had occurred around them. As the grooves elongated distally, their proximal ends became pinched off into pits in the manner described above. This pattern of deeper claustration in the older, more central parts of the infestation, becoming shallower outwards in all directions, is critical to support the contention that infestation took place on a live zoarium and that adjacent zooids were immediately stimulated to claustrate. As the stolons radiated, they overgrew and killed zooids in their path, whilst adjacent ones were stimulated to grow up around the invader. The pattern of stimulation to claustrate therefore proceeded centrifugally. But if overgrowth were effected by an advancing wall of zoecia proceeding inwards from the perimeter or from one side of a damaged area, then the pattern of claustration would have proceeded centripetally or sideways across the infester.

As the initial stolons radiated and diverged from the centre, they branched so as to utilize space efficiently. Thus grooves and lines of pits also branch. In mature infestations, individual stolons can only be distinguished round the edge. The centre appears to be a mass of equispaced pits, but only those laid down on the same stolon are connected by tunnels.

SYSTEMATIC PALAEOLOGY

The arrays of holes that we describe here are the result of modification of the growth pattern of a bryozoan by the presence of a soft-bodied parasite. We choose to regard such bioclastration structures as trace fossils because others have done so before us (Bromley 1970; Müller 1962), and because they may share similarities and intergrade with borings. However, they differ from the popular perception of trace fossils as indicators of animal behaviour. Other dwelling-structures require work to have been perpetrated by the constructor in the form of boring or burrowing activity. Bioclastration structures result from the mere existence of the infester, coupled with modification of the growth behaviour of the host. The end result is likely to mimic accurately the

TEXT-FIG. 4. Camera lucida sketch of pits and grooves of holotype of *Catellocaula vallata* ichnogen. and ichnosp. nov. in external surface of *Amplexopora persimilis*. USNM 419443, scale in mm.



external shape of the parasite, and could be thought of as a biologically formed external mould of its body. Many borings also have this property (clionid sponges, acrothoracican barnacles, clenostome bryozoans, thallophytes), but are now regarded as trace fossils (Bromley 1970).

Ichnogenus CATELLOCAULA nov.

Type species. *Catellocaula vallata* ichnosp. nov.

Derivation of name. Latin: *catella* = little chain; *caula* = hole.

Diagnosis. Bioclaustration structure in bryozoans, consisting of a group of pits sunk into the surface of the zoarium. Pits *c.* 2 mm diameter, up to *c.* 2 mm deep; in plan view pit mouth subcircular to oval with slightly to strongly fluted edges; pit walls may extend up above bryozoan surface to form low thickened rim around pit mouth. Mature specimens consist of arrays of up to thirty or more such pits; in centre of array, pits spaced evenly, *c.* 2–3 mm apart; towards periphery, pits lie equispaced along straight or gently curving lines, each often terminating in a groove, *c.* 2 mm wide, several millimetres long; groove shallows distally so that outer end merges imperceptibly with surface of surrounding zoarium. Floors of adjacent pits along line joined by tunnels, *c.* 2 mm wide, 0.5 mm high. Lines increase in number by bifurcation.

Catellocaula vallata ichnosp. nov.

Plate 87; text-figs. 1–4

Type material. Holotype: USNM 419443 (text-fig. 4); paratypes: USNM 419444–419462. Number prefix USNM refers to collections of United States National Museum, Smithsonian Institution, Washington DC, where all material is housed.

Additional material. Probable additional examples of *C. vallata* occur in poorly silicified ?*Peronopora* (which cannot therefore be sectioned to confirm the identification), from the Clays Ferry Formation near Lexington, Kentucky (USNM 419463–419473).

Type locality. Original label on the holotype states it was collected from the 'Eden (McMicken)' of Newport, Kentucky, USA. This is equivalent in modern nomenclature to the upper part of the Kope Formation (Weir *et al.* 1984).

Derivation of name. Latin: *vallatum* = surrounded with a rampart.

Occurrence. Kope Formation (Edenian = Caradocian, Upper Ordovician); widespread in the vicinity of Cincinnati, Ohio, USA.

Diagnosis. As for genus.

ZOOLOGICAL INTERPRETATION

The soft-bodied organism that provoked the bioclastration response of the trepostome bryozoans was a sessile, stoloniferous, colonial form. The scalloped margin of the pits may indicate that the larger portions of the colony were lobed. The colony could apparently survive the effects of partial envelopment by the bryozoan zooecia, and it is found on all sides of erect zoaria, so it was probably not photosynthetic.

Two Recent groups of organisms may provide models for a palaeobiological reconstruction of this bryozoan parasite. Hydroids (Phylum Cnidaria) sometimes produce horizontal, root-like stolons, termed hydrorhizae, from which arise single upright polyps or branches of polyps. Most colonial hydroid stolons are covered by a non-living chitinous envelope called the perisarc (Barnes 1987), but are much smaller than those described here. Ascidiacian tunicates (Subphylum Urochordata) also include stoloniferous colonial forms most notably the living genus *Perophora*. These tunicates are covered by a cellulose-rich tissue (the tunic). The scalloped pit margins of *C. vallata* strongly evoke the image of compound ascidiacians, especially the living *Botryllus* (see Abbott and Newberry 1980) and the fossil *Palaeobotryllus taylori*, preserved as phosphatic microfossils in the Upper Cambrian of Nevada (Müller 1977). Both shape and size of these forms correspond to the pseudoborings we describe here, and we favour a tunicate origin for *C. vallata*.

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